South African Journal of Botany 97 (2015) 25–31

Contents lists available at ScienceDirect

South African Journal of Botany

journal homepage: www.elsevier.com/locate/sajb

The impact of invasive alien *Prosopis* species (mesquite) on native plants in different environments in South Africa

Ross T. Shackleton [a,*], David C. Le Maitre [a,b], Brian W. Van Wilgen [a], David M. Richardson [a]

[a] Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Matieland 7602, South Africa
[b] Natural Resources and the Environment, CSIR, P.O. Box 320, Stellenbosch 7599, South Africa

ARTICLE INFO

Article history:
Received 28 July 2014
Received in revised form 2 December 2014
Accepted 5 December 2014
Available online 14 January 2015

Edited by J Flores Rivas

Keywords:
Basal area
Biological invasions
Impacts
Invasive plants
Tree invasions

ABSTRACT

Many *Prosopis* species have been introduced to South Africa; some taxa and their hybrids have naturalised and become widespread invasive trees. These invasions have detrimental effects on biodiversity, ecosystem services and human livelihoods. Although several studies have documented these impacts, the studies have been limited to single sites or restricted areas. This study assessed the *Prosopis* population across the full invasive range of the genus in South Africa, and quantified the effects of invasions on native woody and herbaceous species. Basal areas of invasive *Prosopis* stands reached 9 m^2/ha, and were on average higher along perennial rivers than along ephemeral rivers (mean basal areas of 3.2 vs. 1.4 m^2/ha). Native woody species density, basal area, richness and diversity all decreased significantly as the basal area of *Prosopis* stands increased. For example, up to eight native woody species occurred at basal area of <2 m^2/ha, this decreased to three native species or fewer at basal areas of >4 m^2/ha. The cover of native perennial grasses and herbaceous plants declined from 15–20% where the basal area of *Prosopis* was <2 m^2/ha to zero where the basal area of *Prosopis* was >4.5 m^2/ha. The results highlight the widespread nature of the impacts across all invaded biomes. Current control of *Prosopis* has had limited success, and alternative, potentially more effective, options are controversial. In the light of the widespread impacts, we recommend that a thorough assessment of the problem be undertaken to inform policy.

1. Introduction

Many 'multi-purpose' trees have been transported around the world and several have subsequently become naturalised and invasive (Rejmánek and Richardson, 2013). Tree invasions have become much more widespread in recent decades in many parts of the world and several invasive alien trees are key drivers of biodiversity loss and disruption of ecosystem functioning (Richardson et al., 2014). *Prosopis* (mesquite) taxa are widespread invaders in semi-arid and arid areas across the world (Pasiecznik et al., 2001). These invasions have detrimental impacts on the environment, society and local economies (Shackleton et al., 2014). Negative impacts of *Prosopis* invasions on a wide range of native organisms have been documented in many parts of the world. These include reductions in plant species richness, density and diversity in Hawaii, India, Kenya and the United Arab Emirates (El-Keblawy and Al-Rawai, 2007; Kaur et al., 2012; Muturi et al., 2013), increased native tree mortality in Brazil and South Africa (Schachtschneider and February, 2013; de Souza Nascimento et al., 2014; Shackelton et al., 2015), negative impacts on bird and insect community composition in South Africa (Steenkamp and Chown, 1996; Dean et al., 2002) and reductions in turtle and bird recruitment on Atlantic islands (Belton, 2008). Ecosystem services such as soil quality, grazing and water supply are affected by *Prosopis* invasions, leading to a range of negative consequences for local human communities (Geesing et al., 2004; Mwangi and Swallow, 2005; Ndhlovu et al, 2011; Wise et al., 2012; Dzikiti et al., 2013; Ayanu et al., 2014; Shackleton et al., 2014).

Prosopis species were introduced to South Africa in the late 1800s and were widely distributed and planted up to the 1960s for shade and fodder during a time of severe drought (Harding and Bate, 1991; Zimmermann, 1991; Poynton, 2009). Invasive *Prosopis* stands (comprising several species and their hybrids) now cover very large areas of arid and semiarid parts of the country, with extensive invasions in the Northern Cape and Western Cape provinces (Poynton, 2009). *Prosopis* is estimated to have invaded 1.8 million ha (1.5%) of South Africa and has been estimated to spread between 3.5 and 8% per annum (Coetsee, 1993; Harding and Bate, 1991; Versfeld et al., 1998). This implies that invaded areas can double every 5–8 years. In the Northern Cape province *Prosopis* invasions increased by almost 1 million ha between 2002 and 2007, which is equivalent to 27.5% per year (Van Den Berg, 2010). In terms of land area invaded, *Prosopis* is ranked as the second worst invasive alien plant taxon in South Africa after Australian *Acacia* species (Henderson, 2007). The genus also ranks highly for its negative impacts on biodiversity and ecosystem services (Le Maitre et al., 2000). Invasive

* Corresponding author.
E-mail addresses: rtshackleton@gmail.com (R.T. Shackleton), dlmaitre@csir.co.za (D.C. Le Maitre), bvanwilgen@sun.ac.za (B.W. Van Wilgen), rich@sun.ac.za (D.M. Richardson).

http://dx.doi.org/10.1016/j.sajb.2014.12.008
0254-6299/

Prosopis species are being managed by the Working for Water programme in South Africa, using mechanical and chemical and biological control (three seed-feeding beetle species) but with limited success in reducing the overall extent of invasions and their impacts (Zachariades et al., 2011; Van Wilgen et al., 2012).

Ecosystem services such as water supply and grazing potential are clearly affected by *Prosopis* invasions in South Africa (Ndhlovu et al., 2011; Wise et al., 2012; Dzikiti et al., 2013). Further negative effects are noted on bird and insect species richness and composition in the Kalahari (Steenkamp and Chown, 1996; Dean et al., 2002). *Prosopis* also increases the mortality of a keystone tree species (*Acacia erioloba*) in the Kalahari Desert (Schachtschneider and February, 2013). All of these studies have been limited to small areas or single sites, and there is a need for more extensive surveys to establish both the nature of the invasions, and the degree of impact that they are having in different biomes and habitats. Such information would be necessary for estimating the impacts of *Prosopis* over large spatial areas, and for informing large-scale management strategies.

This study aimed (1) to quantify the basal areas of *Prosopis* invasions in different biomes and river types across South Africa; and (2) to assess the impacts of *Prosopis* invasion on native plant species richness, diversity, basal area, density and cover over a wide area representative of the invasive range of the genus in South Africa.

2. Methods

2.1. Scope of investigation and study sites

We investigated the degree of variation in the basal area of invasive *Prosopis* trees at 11 sites across three biomes (Nama Karoo, Savanna and Succulent Karoo, see Mucina and Rutherford, 2006) and three river classes (see below). We used the same sites to investigate the effects of *Prosopis* invasion on the composition and structure of indigenous plant communities. These sites covered most of the range of invasive alien *Prosopis* trees in South Africa. Mean annual rainfall varied between 150 and 450 mm, and the seasonality of rainfall differed, with rain falling either predominantly in winter or summer, or evenly distributed across seasons (Dent et al, 1989) (Fig. 1). Rainfall was higher in the Succulent Karoo and Savanna study sites and lowest in the Nama Karoo study sites (Fig. 1). The underlying geology of the area included shales of the Dwyka and Ecca Group, granites of the Namaqua group in the east, gneiss of the Namaqua and Natal Metamorphic Provinces, deep sands of the Kalahari Group in the central and northern sites, shales of the Transvaal Supergroup in the east, and shales of the Beaufort group in the south (Voster, 2003). Altitudes ranged from 700 to 1300 m above sea level.

2.2. Data collection

At each of the 11 sites, we set out transects on farms that had uninvaded vegetation, as well as areas invaded by different densities of *Prosopis*. Along each transect, three plots of 10 × 10 m were placed at 50 m intervals. In total, we evaluated 894 plots, selected to cover a gradient from uninvaded to heavily-invaded sites. Care was taken not to place transects in disturbed areas so as to exclude, as far as possible, the influence of past land practises. On each plot, we measured the stem diameters of all trees and shrubs with stems >1 cm diameter at 30 cm above the ground. Diameters were measured at 30 cm, and not at breast height, as the trees in the study site often branched below breast height. In the first plot of each transect the percentage cover of perennial grass, annual grass, perennial herbaceous plants, annual herbaceous plants, organic litter and bare ground was visually estimated by averaging estimated cover on four 1 × 1 m quadrats placed in the centre of each quarter of the plot. Individual herbaceous species were not identified. *Prosopis* trees were not recorded at species level as most stands comprised complex hybrid mixtures that are difficult to identify (Mazibuko, 2012).

We also classified the habitat type for each transect into one of three categories: floodplains of perennial rivers (the Orange River, with permanent flow year-round); floodplains of larger ephemeral rivers (drainage lines with seasonal flow, listed by the Water Institute of South Africa (WISA), www.ewisa.co.za/misc/riverssa/defaultb.htm); and smaller (tributary) ephemeral rivers (those not listed by WISA). Data were collected in the austral winter between June and September 2013.

2.3. Data analysis

2.3.1. Prosopis density and basal area across different environments

We investigated whether the basal area of *Prosopis* invasions differed between the river categories (perennial, large ephemeral, or

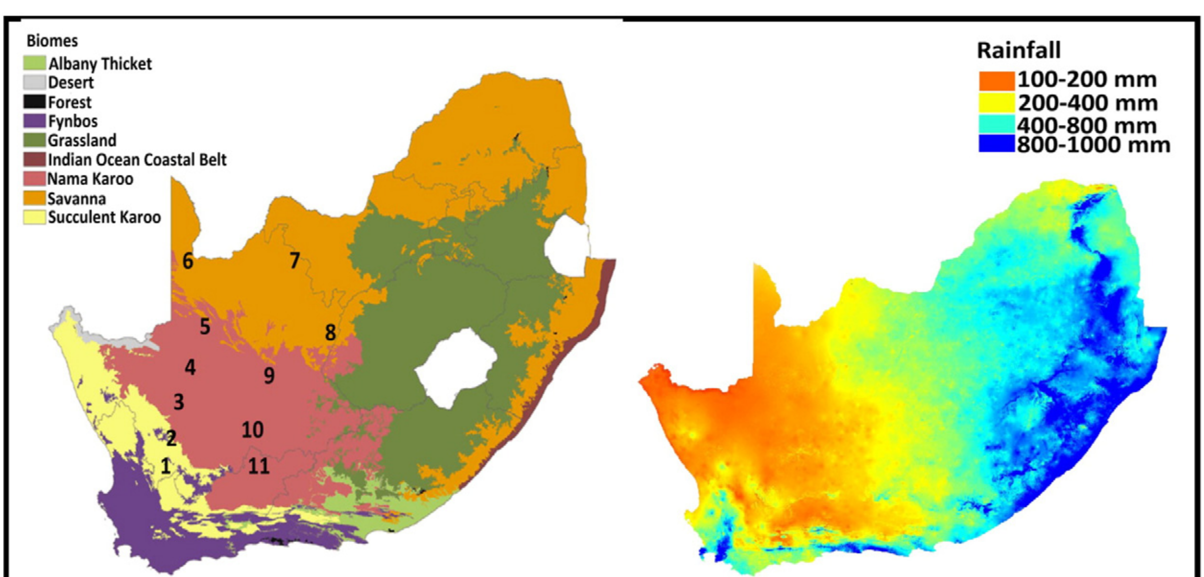

Fig. 1. Study area showing biomes, mean annual precipitation and data collection sites across South Africa: (1) Calvinia; (2) Loeriesfontein; (3) Brandvlei; (4) Kenhardt; (5) Upington; (6); Mier (7) Seven; (8) Kimberley; (9) Prieska; (10) Carnavon; and (11) Beaufort West.

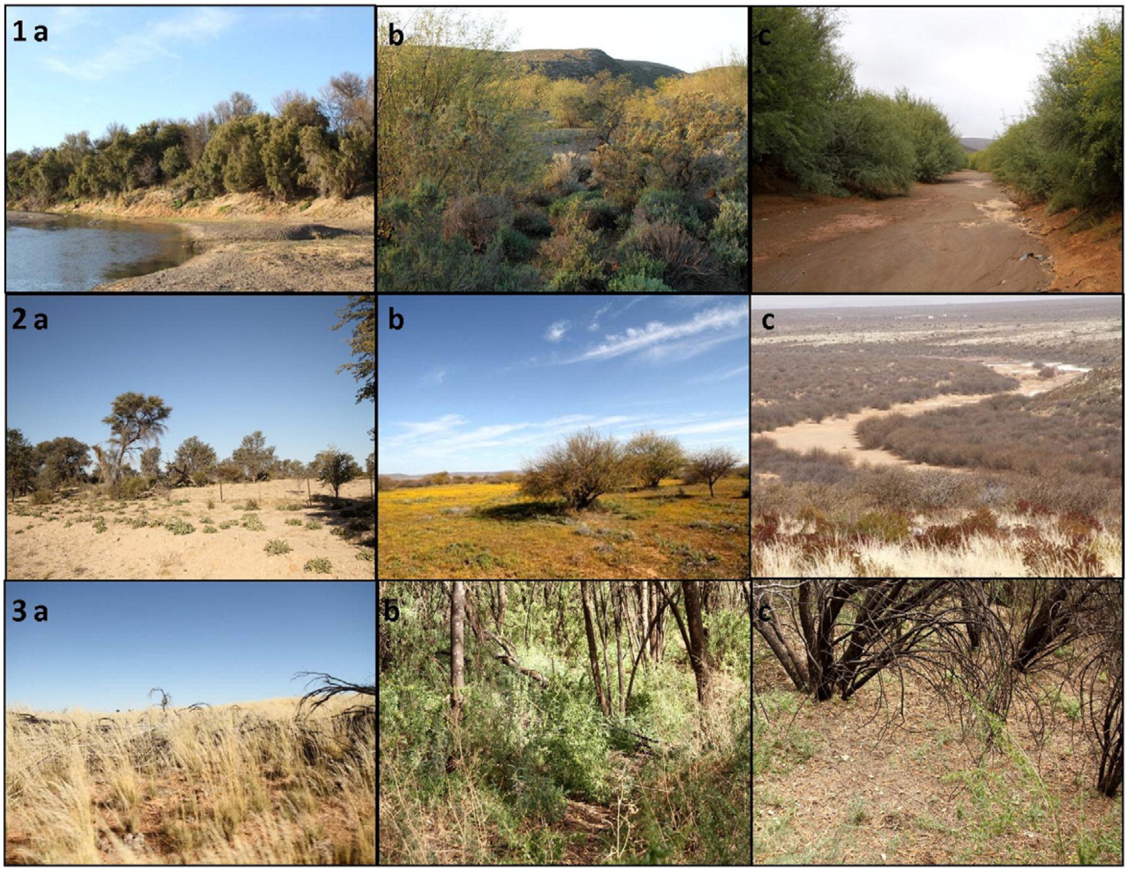

Fig. 2. Images of *Prosopis* and native vegetation in South Africa: Panel 1 — (a) non-invaded riverine forest; (b) low *Prosopis* invasion; (c) dense *Prosopis* invasion; Panel 2 — (a) non-invaded Savanna vegetation; (b) sparse *Prosopis* invasion; (c) landscape scale, dense *Prosopis* invasion; Panel 3 — (a) grass cover 5 years after clearing *Prosopis*; (b) ground cover under native *Acacia karroo* riverine forest; (c) ground cover under a *Prosopis* invasion.
Photos: R T. Shackleton

small ephemeral) and between ephemeral rivers in the three biomes (Nama Karoo, Savanna and Succulent Karoo). In each river category, and in each biome, plots were ranked from the lowest to highest basal area, and divided into three groups of equal size, representing low, moderate and high basal area classes. Welch ANOVAs and Games–Howell Post-Hoc tests were used to compare *Prosopis* in the different basal area classes across biomes and river categories. Welch ANOVAs and Games–Howell tests were used because the assumption of homogeneity of variances was not met.

2.3.2. Impacts of Prosopis invasions on native species

The effects of *Prosopis* basal area on the relative abundance of native woody species were investigated using the Shannon–Wiener index (a measure of relative dominance, Magurran, 2004). Regressions were run to compare the relationship between the basal area of *Prosopis* invasions and the density, basal area, species richness and diversity of native woody species. Regressions were also used to examine the effect of *Prosopis* basal area on the cover of grasses, herbaceous plants, organic litter and bare ground cover.

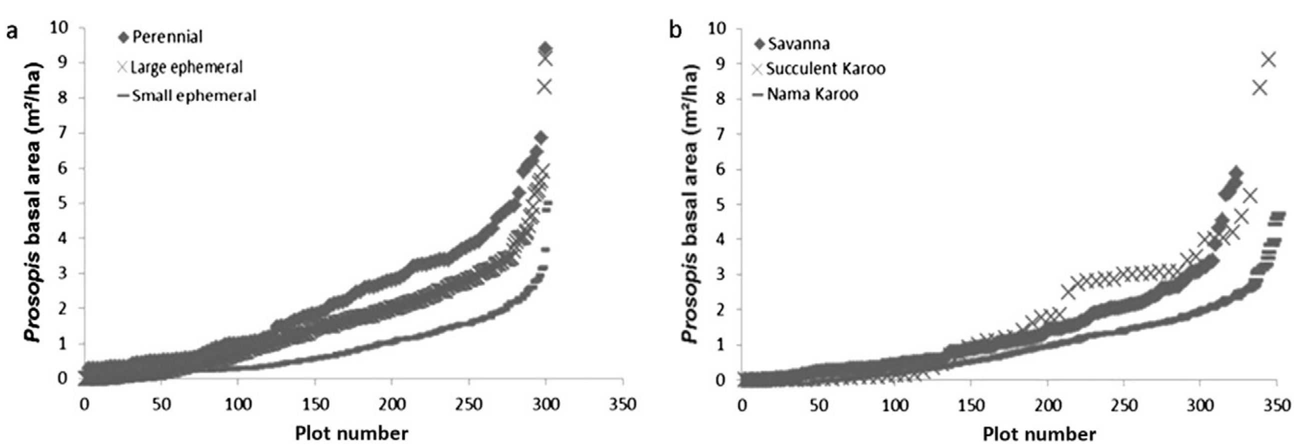

Fig. 3. A comparison of *Prosopis* basal area across: (a) three river size classes; and (b) three biomes. Data points are for individual plots ranked from low to high in terms of basal area. As the number of plots differed between river classes and biomes, the horizontal axis was scaled to facilitate comparison.

Table 1
Mean (± standard error) basal area (m^2/ha) of invasive *Prosopis* species in three habitat types (river categories). Basal area values were ranked and divided into three data sets of equal size representing low, moderate and high basal areas respectively. The letters represent significant differences between groups according to Games Howell Post-Hoc tests.

Basal area class	River category			p-Value
	Perennial	Large ephemeral	Small ephemeral	
Low	1.01 ± 1.25^a	0.69 ± 0.94^a	0.25 ± 0.32^b	$F = 78.5$, df = 2, $p < 0.0001$
Moderate	1.69 ± 1.75^a	1.71 ± 1.23^a	0.83 ± 0.79^b	$F = 86.33$, df = 2, $p < 0.0001$
High	3.2 ± 1.58^a	2.41 ± 1.44^b	1.43 ± 0.71^c	$F = 79.77$, df = 2, $p < 0.0001$

3. Results

3.1. Effects of biome and habitat type on Prosopis basal area

Of the 894 plots enumerated, 220 plots were free of *Prosopis* trees. When the remaining dataset (plots with *Prosopis* trees of varying basal area) were ranked from the lowest to the highest basal area of *Prosopis* trees, the plots in the first third (low basal area) had a mean basal area of 0.57 ± 0.97 m^2/ha for all sites across South Africa. Corresponding values for moderate and high basal area plots were, 1.14 ± 1.12 m^2/ha in the middle range and 2.17 ± 1.31 m^2/ha in the high range (Fig. 2).

Habitat type (river categories) had significant effects on the basal area of *Prosopis* stands (Fig. 3a, Table 1). On average, the plots in the high-range class had more than double the basal area along perennial rivers than along both categories of ephemeral rivers (3.2 vs. 1.43 m^2/ha). Small ephemeral rivers also tended to have lower mean basal areas in the medium and low ranges, compared to large ephemeral or perennial rivers.

The effects of biome type on the basal area of *Prosopis* invasion were less clear (Fig. 3b, Table 2). On average, the high range plots differed significantly between all three biomes. The Succulent Karoo (wetter) had more than double the basal area of the Nama Karoo (3.84 vs. 1.87 m^2/ha), while the value for the Savanna biome was intermediate (2.04 m^2/ha).

3.2. Effects of invasion by Prosopis on native woody plants

Invasion by *Prosopis* reduced the density, basal area, richness and diversity of native woody plants (Fig. 4). Native woody species density, basal area, richness and diversity all decreased significantly ($p < 0.0001$) as the basal area of *Prosopis* stands increased. Where *Prosopis* trees were either absent or present at basal areas of less than 4 m^2/ha, native woody trees were able to persist at densities above 4000 stems/ha; as invasions increased above basal areas of greater than 4 m^2/ha, the maximum density of native woody species fell rapidly to between 2000 and zero trees per ha. The number of native woody species present on the plots also declined, from five–eight species where *Prosopis* was at basal areas below 2 m^2/ha, to one–three species when the basal area of invasions exceeded 4 m^2/ha. As the basal area of invasions increased, stands were correspondingly more dominated by *Prosopis*, as indicated by Shannon–Wiener indices as low as zero (indicating total dominance by a single species) in highly invaded stands. The scatter plots (Fig. 4) suggest two thresholds, one where *Prosopis* basal area of invasions reach 2 m^2/ha (after which native tree populations drop substantially but are still present) and a second at where the basal area reaches 6 m^2/ha (after which native trees are largely eliminated).

3.3. Effects of Prosopis invasion on native herbaceous plant and abiotic ground cover

Invasion by *Prosopis* reduced the cover of perennial grasses and herbaceous plants (Fig. 5). As was the case with native woody plants, the cover of perennial grasses dropped from above 15% where the basal area of *Prosopis* was below 2 m^2/ha, to zero where the *Prosopis* basal area was above 4.5 m^2/ha. Similarly, the cover of native perennial herbaceous plants dropped from above 20% where the basal area of *Prosopis* was below 2 m^2/ha, to zero where the *Prosopis* basal area was above 4.5 m^2/ha. On the other hand, we were not able to detect any meaningful impacts of invasion by *Prosopis* on the cover of annual grasses and annual herbaceous plants. Native annual plants persisted at quite high levels of invasion by *Prosopis*. Organic litter cover and bare ground cover was also not significantly influenced by *Prosopis* invasion (Fig. 6).

4. Discussion

4.1. International comparisons

The findings of our study are similar in many ways to those made for *Prosopis* invasions in other parts of the world. *Prosopis* forms dense invasive thickets across much of South Africa's interior. These invasive thickets are influenced by abiotic factors, and areas with higher water availability have higher invasions with higher basal areas (Fig. 3). Similarly, densities of invasive *Prosopis pallida* were 5.3 times greater in relatively moist lowlands in Hawaii, compared to drier upland plots (Dudley et al., 2014). Dudley et al. (2014) also showed that greater water accessibility increased nitrogen fixation, which was linked to increased growth and productivity of these *Prosopis* invasions. This trend is mirrored in findings by Stromberg

Table 2
Mean (± standard error) basal area (m^2/ha) of invasive *Prosopis* species in three biomes. Basal area values were ranked and divided into three datasets of equal size representing low, moderate and high basal areas respectively. The letters represent significant differences between groups according to Games Howell Post-Hoc tests.

Basal area class	Biome			p-Value
	Nama Karoo	Savanna	Succulent Karoo	
Low	0.34 ± 0.41^a	0.40 ± 0.47^b	0.16 ± 0.29^c	$F = 39.9$, df = 2, $p < 0.0001$
Moderate	1.15 ± 0.82^a	1.47 ± 1.17^a	1.55 ± 1.10^a	$F = 45.22$, df = 2, $p < 0.095$
High	1.87 ± 0.89^a	2.04 ± 1.40^b	3.84 ± 2.00^c	$F = 29.95$, df = 2, $p < 0.0001$

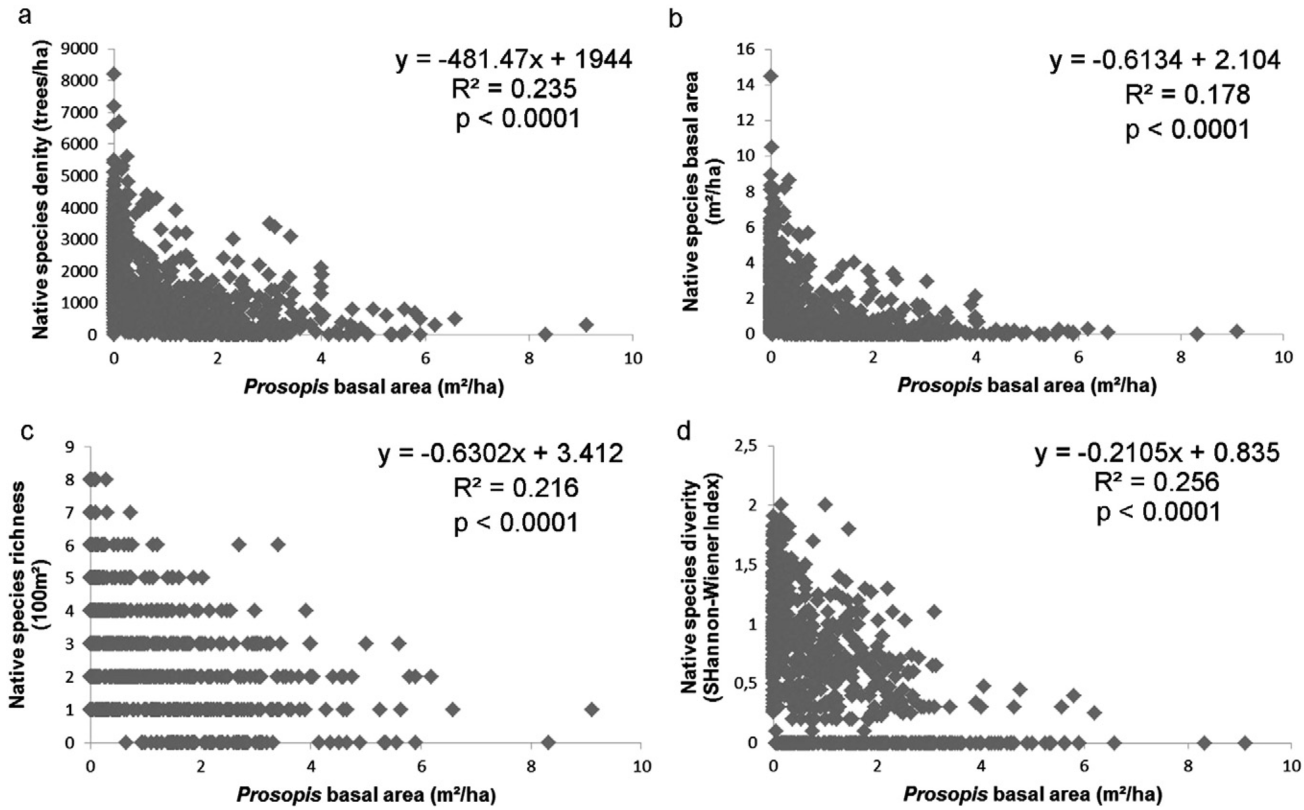

Fig. 4. Scatter plots and regression analyses showing the effects of *Prosopis* basal area on: (a) native woody species density; (b) basal area; (c) species richness; and (d) Shannon–Wiener species diversity index.

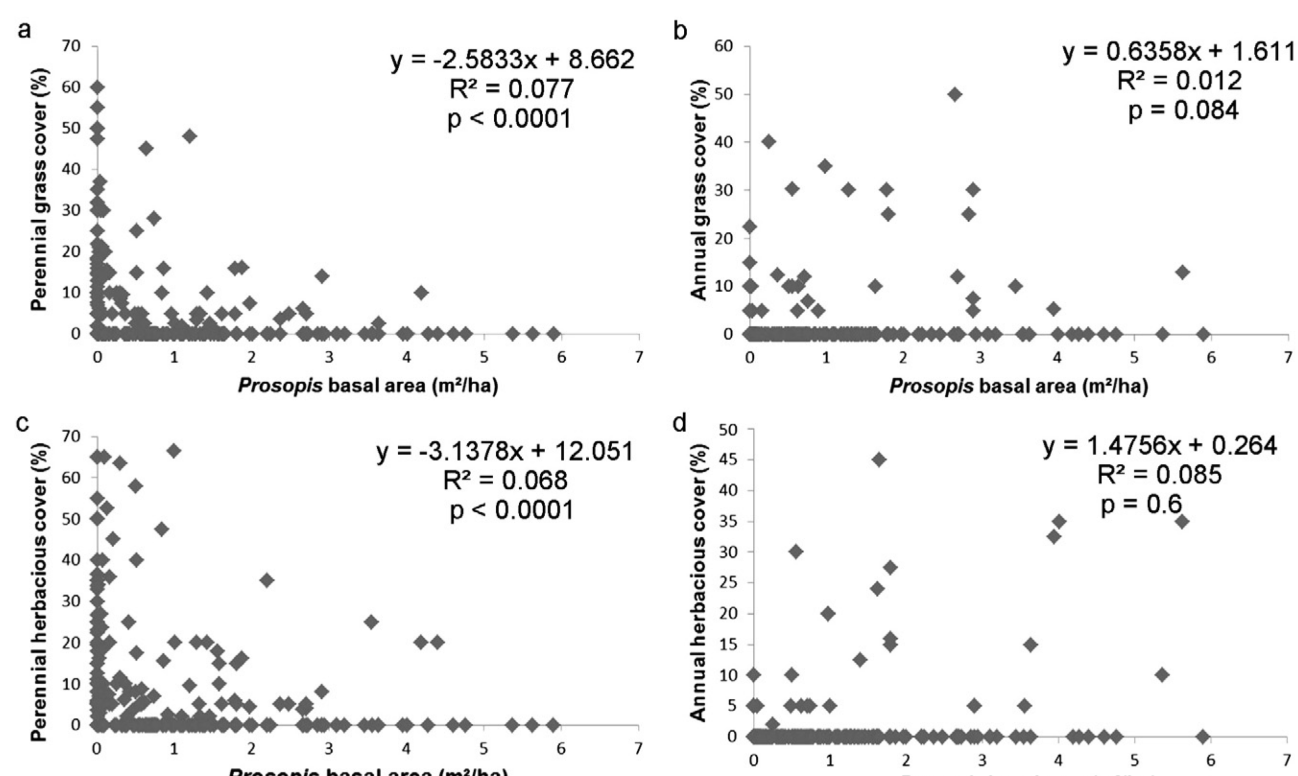

Fig. 5. Scatter plots and regression analysis assessing the effect of *Prosopis* basal area on non-woody plant cover: (a) perennial grass cover; (b) annual grass cover; (c) perennial herbaceous plant cover (100 m^2); and (d) annual herbaceous plant cover.

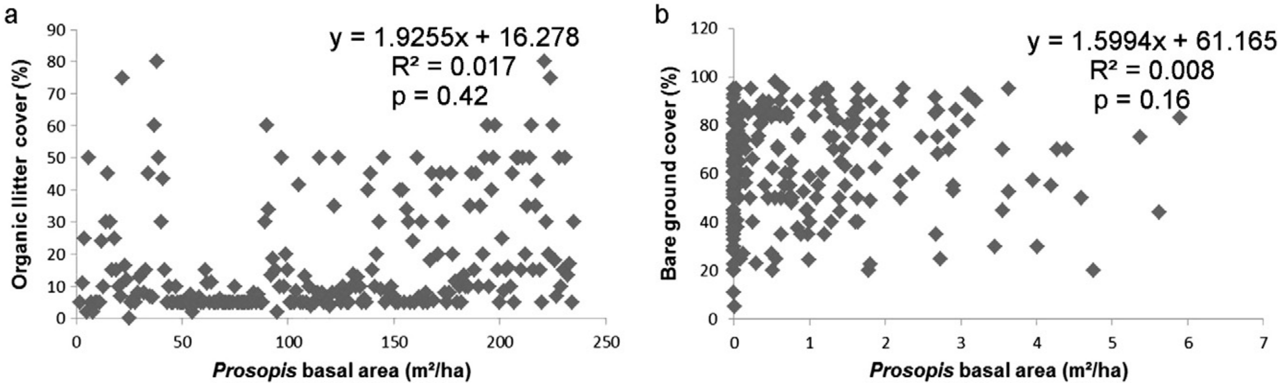

Fig. 6. Scatter plots and regression analyses showing the effect of *Prosopis* basal area on (a) organic litter cover; and (b) bare ground cover.

et al. (1993) who showed that weedy (native invasive) *Prosopis velutina* invasions in the Sonoran Desert have higher basal areas in perennial-riparian compared to xero-riparian (ephemeral rivers) and upland areas. These findings show that *Prosopis* responds in a similar way, whether as a weed in its native range or where it is an invasive alien tree.

Our findings showing the negative impacts of *Prosopis* invasions on native plants (Figs. 4 and 5) are supported by other studies internationally. *Prosopis* invasions also negatively affected native species richness in Hawaii, India, Kenya and the United Arab Emirates (El-Keblawy and Al-Rawai, 2007; Kaur et al., 2012; Muturi et al., 2013). In the United Arab Emirates, native species richness and densities under *Prosopis* tree canopies were lower than at canopy margins and away from *Prosopis* canopies (El-Keblawy and Al-Rawai, 2007). This suggests that *Prosopis* was able to outcompete native plants for limited resources, such as light and water (Garcia-Serrano et al., 2007; El-Keblawy and Al-Rawai, 2007). The allelopathic effects of *Prosopis* have also been shown to reduce native tree germination and survival (de Souza Nascimento et al., 2014; ElEl-Keblawy and Abdelfatah, 2014). Our results for woody plants differed from those in Australia where it was found that *Prosopis* invasions had a positive effect on the density of native tree species but a negative effect on density of native shrub species (Van Klinken et al., 2006). The only trees found in areas with *Prosopis* invasion in Australia (*Eucalyptus* spp.) showed higher densities in dense and moderate *Prosopis* invasions than in areas with low-density invasions (Van Klinken et al., 2006). A similar trend of *Prosopis* presence increasing native species richness and diversity was also found in India, however, the increase was in weedy, economically unimportant native species and there were negative impacts on endangered *Commiphora wightii* and other important climax native species (Kumar and Mathur, 2014). Percentage cover of native grass and herbaceous plant species is also reduced by *Prosopis* invasions (Fig. 5). Similar shifts were seen in Australia, with far fewer shrubs and grasses found in densely invaded areas (Van Klinken et al., 2006). Denser *Prosopis* invasions tended to an increase in bare ground cover (Fig. 6). Loss of ground cover under *Prosopis* invasions has been seen to facilitate soil erosion in some areas (Bedunah and Sosebee, 1986).

4.2. Implications of findings

Our study has added to the growing body of evidence (Steenkamp and Chown, 1996; Dean et al, 2002; Ndhlovu et al., 2011; Dzikiti et al., 2013; Schachtschneider and February, 2013) that invasion by *Prosopis* has negative impacts on South Africa's natural ecosystems and the services that they deliver. We have further demonstrated that these impacts occur across a wide area, in all biomes invaded by *Prosopis* trees. While *Prosopis* trees were originally introduced to provide fodder, and for other benefits, recent studies suggest that these benefits are rapidly being eroded by negative impacts (Wise et al., 2012). Loss of native plants due to *Prosopis* invasions not only decreases biodiversity in the area, but also has negative implications for local livelihoods. Many people in the rural areas of South Africa rely on natural resources from plants for incomes and subsistence (Shackleton et al., 2007). *Prosopis* reduces the densities of native species like *Acacia erioloba* and *Acacia karroo* which are highly valued and commonly used for firewood and fodder in South Africa (Powell, 2001; Pote et al., 2006). This is of particular importance as many communities dislike *Prosopis* for fuelwood (Geesing et al., 2004). The loss of native grass and herbaceous plant cover also decreases the grazing potential in invaded areas (Ndhlovu et al., 2011). This has serious repercussions for the local economy of these arid and semiarid parts of the country, considering that livestock agriculture is the primary land use and one of the key factors driving the economy and employment in these areas.

Wise et al. (2012) noted that, while the estimated net economic value of mesquite was substantial, this value was being eroded as invasions grow, with net negative values expected within 4–22 years, depending on the rate of spread. In response to the growing threat, the South African government has spent R 435 million (between 1996 and 2008) on mechanical control operations aimed at clearing stands of invasive *Prosopis* trees in arid areas (Van Wilgen et al., 2012). In addition, biological control agents were released between 1983 and 1997 in attempts to control *Prosopis* (Zachariades et al., 2011). However, because of the perceived value of *Prosopis* trees, biological control attempts were confined to seed-feeding insects that would not damage the trees. As a result, the degree of control achieved by these insects is currently inadequate to stem the spread. Other biological control agents that have been deemed safe to release in South Africa have showed success in limiting *Prosopis* invasions in Australia (Van Klinken, 2012). The mechanical control programme has been equally ineffective at a broad scale, as evidenced by the rapid population growth over the past two decades (Van den Berg, 2010). Despite substantial investment, mechanical control efforts were only able to treat about 0.6% of the estimated invaded area each year (Van Wilgen et al., 2012), which is way below the spread rate of the species.

It is clear that *Prosopis* invasions will continue to spread despite intensive attempts at control and the impacts will grow accordingly, unless more effective ways can be found to control the genus in South Africa. One obvious solution would be to explore the feasibility of introducing more damaging biological control agents that would be more effective at curtailing spread, such *Evippe* spp. (Van Klinken, 2012). There is some resistance to this idea (particularly further north in Africa), because there is a risk that biological control agents could attack indigenous African species of *Prosopis*, or other alien *Prosopis* species that are not invasive, and that are useful (Zachariades et al., 2011). Other proposals include the notion of utilization as a control method (Pasiecznik et al., 2006; Shackleton et al., 2014). For example, many people rely on *Prosopis* for their livelihoods in India, where it has been suggested that increased use of products from *Prosopis* through proper silviculture would be a feasible way of managing costs and improving benefits relating to these invasions (Walter and Armstrong, 2014). However, use in South Africa is lower and the silviculture option would not be feasible (Shackelton et al., in press). These suggestions are also controversial as their effectiveness is disputed and they create a dependence on the resource which provides justification for further distribution of the invasive species (Geesing et al., 2004; Van Wilgen and Richardson, 2014). The growing evidence, presented in this study and elsewhere, of the widespread negative impacts of *Prosopis* invasions will continue to increase unless a solution can be found. We recommend that a full assessment of the costs and benefits be carried out to inform policy decisions. The creation of national strategic plans such as those in Australia would also help to guide management and aid in efficiency in the future. Such an assessment would have to be carried out with a political mandate (for legitimacy), involve all of the stakeholders, and use experts and peer review to address all of the issues.

Acknowledgements

Funding for this work was provided by the DST-NRF Centre of Excellence for Invasion Biology and the Working for Water Programme through their collaborative research project on "Integrated management of invasive alien species in South Africa". DMR acknowledges additional support from the National Research Foundation (grant 85417) and the Oppenheimer Memorial Trust. Thank you to the farmers who gave use access to their land and were so helpful.

References

Ayanu, Y., Jentsch, A., Müller-Mahn, D., Rettberg, S., Romankiewicz, C., Koellner, T., 2014. Ecosystem engineer unleashed: *Prosopis juliflora* threatening ecosystem services? Regional Environmental Change http://dx.doi.org/10.1007/s10113-014-0616-x.

Bedunah, D.J., Sosebee, R.E., 1986. Influence of mesquite control on soil erosion on a depleted range site. Journal of Soil and Water Conservation 41, 131–135.

Belton, T., 2008. Management Strategy for Mexican Thorn (*Prosopis juliflora*) on Ascension Island: An Assessment of This Species, and Recommendations for Management. RSPB, Bedfordshire.

Coetsee, J., 1993. Prosopis vervuil Karoo. Landbouweekblad, South Africa.

de Souza Nascimento, C.E., Tabarelli, M., da Silva, C.A.D., Leal, I.R., de Souza Tavares, W., Serrãno, J.E., Zanuncio, J.C., 2014. The introduced tree *Prosopis juliflora* is a serious threat to native species of the Brazilian Caatinga vegetation. Science of the Total Environment 481, 108–113.

Dean, W.R.J., Anderson, M.D., Milton, S.J., Anderson, T.A., 2002. Avian assemblages in native *Acacia* and alien *Prosopis* drainage line woodland in the Kalahari, South Africa. Journal of Arid Environments 51, 1–19.

Dent, M.C., Lynch, S.D., Schulze, R.E., 1989. Mapping Mean Annual and Other Rainfall Statistics over Southern Africa. Water Research Commission, Pretoria WRC Report 109/1/89. pp 230.

Dudley, B.D., Hughes, R.F., Ostertag, R., 2014. Groundwater availability mediates the ecosystem effects of an invasion of Prosopis pallida. Ecological Applications 24, 1954–1971. http://dx.doi.org/10.1890/13-1262.1.

Dzikiti, S., Schachtschneider, K., Naiken, V., Gush, M., Moses, G., Le Maitre, D.C., 2013. Water relations and the effects of clearing invasive *Prosopis* trees on groundwater in an arid environment in the Northern Cape, South Africa. Journal of Arid Environments 90, 103–113.

El-Keblawy, A., Abdelfatah, M.A., 2014. Impacts of native and invasive exotic *Prosopis* congeners on soil properties and associated flora in the arid United Arab Emirates. Journal of Arid Environments 100, 1–8.

El-Keblawy, A., Al-Rawai, A., 2007. Impacts of the invasive exotic *Prosopis juliflora* (Sw.) D.C. on the native flora and soils of the UAE. Plant Ecology 190, 23–35.

Garcia-Serrano, H., Sans, F.X., Escarré, J., 2007. Interspecific competition between alien and native congeneric species. Acta Oecologica 31, 69–78.

Geesing, D., Al-Khawlani, M., Abba, M.L., 2004. Management of introduced *Prosopis* species: can economic exploitation control and invasive species? Unasylva 217, 36–44.

Harding, G.B., Bate, G.C., 1991. The occurrence of invasive *Prosopis* species in the north-western Cape, South Africa. South African Journal of Science 87, 188–192.

Henderson, L., 2007. Invasive, naturalized and casual alien plants in southern Africa: a summary based on the Southern African Plant Invaders Atlas (SAPIA). Bothalia 37, 215–248.

Kaur, R., Gonzales, W.L., Llambi, L.D., Soriano, P.J., Callaway, R.M., Rout, M.E., Gallaher, J.T., Inderjit, 2012. Community impacts of *Prosopis juliflora* invasion: biogeographic and congeneric comparisons. PLoS One 7, e44966.

Kumar, S., Mathur, M., 2014. Impact of invasion by *Prosopis juliflora* on plant communities in arid grazing lands. Tropical Ecology 55, 233–246.

Le Maitre, D.C., Versfeld, D.B., Chapman, R.A., 2000. The impact of invading alien plants on surface water resources in South Africa: a preliminary assessment. Water SA 26, 397–408.

Magurran, A.E., 2004. Measuring biological diversity. Blackwell, Oxford.

Mazibuko, D.M., 2012. Phylogenetic Relationship of *Prosopis* in South Africa: An Assessment of the Extent of Hybridization, and the Role of Genome Size and Seed Size in the Invasion Dynamics. Masters of Science. Stellenbosch University, Stellenbosch.

Mucina, L., Rutherford, M.C., 2006. The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia. 19. South African National Biodiversity Institute, Pretoria.

Muturi, G.M., Poorter, L., Mohren, G.M.J., Kigomo, B.N., 2013. Ecological impacts of *Prosopis* species invasion in Turkwel riverine forest, Kenya. Journal of Arid Environments 92, 89–97.

Mwangi, M., Swallow, B., 2005. Invasion of *Prosopis juliflora* and local livelihoods: case study from the Lake Baringo area of Kenya . ICRAF Working Paper. 3. World Agroforestry Centre, Nairobi.

Ndhlovu, T., Milton-Dean, S.J., Esler, K.J., 2011. Impact of *Prosopis* (mesquite) invasion and clearing on the grazing capacity of semiarid Nama Karoo rangeland, South Africa. African Journal of Range and Forage Science 28, 129–137.

Pasiecznik, N.M., Felker, P., Harris, P.J.C., Harsh, L.N., Cruz, G., Tewari, J.C., Cadoret, K., Maldonado, L.J., 2001. The *Prosopis juliflora–Prosopis pallida* complex: a monograph. HDRA, Coventry, UK.

Pasiecznik, N.M., Chge, S.K., Muthike, G.M., Chesang, S., Fehr, C., Blackwell-Stone, P., Wright, J., Harris, P.J.C., 2006. Putting Knowledge on *Prosopis* into Use in Kenya. Pioneering Advances in 2006. KEFRI, Nairobi, Kenya and HDRA, Coventry, UK (13 pp.).

Pote, J., Shackleton, C., Cocks, M., Lubke, R., 2006. Fuelwood harvesting and selection in valley thicket, South Africa. Journal of Arid Environments 67, 270–287.

Powell, J., 2001. Utilization of the Camelthorn Tree, in the Kalahari Region. University of Stellenbosch, Conservation Ecology Department, Stellenbosch (Report for BIOTA).

Poynton, R.J., 2009. Tree planting in southern Africa. Other Genera. Department of Agriculture, Forestry and Fisheries. Vol. 3 (Pretoria. South Africa).

Rejmánek, M., Richardson, D.M., 2013. Trees and shrubs as invasive alien species — 2013 update of the global database. Diversity and Distributions 19, 1093–1094.

Richardson, D.M., Hui, C., Nunez, M., Pauchard, A., 2014. Tree invasions — patterns and processes, challenges & opportunities. Biological Invasions 16, 473–481.

Schachtschneider, K., February, E.C., 2013. Impact of *Prosopis* invasion on a keystone tree species in the Kalahari Desert. Plant Ecology 214, 597–605.

Shackelton, R.T., Le Maitre, D.C., Richardson, D.M., 2015. *Prosopis* invasions in South Africa: population structures and impacts on native tree population stability. Journal of Arid Environments 114, 70–78.

Shackelton, R.T., Le Maitre, D.C., Richardson, D.M., 2015. Stakeholder perceptions and practices regarding *Prosopis* (mesquite) invasions and management in South Africa. AMBIO http://dx.doi.org/10.1007/s13280-014-0597-5 (in press).

Shackleton, C.M., Shackleton, S.E., Buiten, E., Bird, N., 2007. The importance of dry woodlands and forests in rural livelihoods and poverty alleviation in South Africa. Forest Policy and Economics 9, 558–577.

Shackleton, R.T., Le Maitre, D.C., Pasiecznik, N.M., Richardson, D.M., 2014. *Prosopis*: a global assessment of the biogeography, benefits, impacts and management of one of the world's worst woody invasive plant taxa. AOB Plants 6, plu027. http://dx.doi.org/10.1093/aobpla/plu027.

Steenkamp, H.E., Chown, S.L., 1996. Influence of dense stands of an exotic tree *Prosopis glandulosa* Benson, on a savanna dung beetle (Coleoptera: *Scarabeidae*) assemblage in southern Africa. Biological Conservation 78, 305–311.

Stromberg, J.C., Wilkins, S.D., Tress, J.A., 1993. Vegetation-hydrology models: implications for management of *Prosopis velutina* (velvet mesquite) riparian ecosystems. Ecological Applications 3, 307–314.

Van den Berg, E.C., 2010. Detection, Quantification and Monitoring *Prosopis* spp. in the Northern Cape Province of South Africa Using Remote Sensing and GIS. MSc Science. North-West University, Potchefstroom.

Van Klinken, R., 2012. *Prosopis* spp. — mesquite. In: Julien, M., McFadyen, R., Cullen, J. (Eds.), Biological control of weeds in Australia. CISRO, Melbourne, Australia, pp. 477–485.

Van Klinken, R.D., Graham, J., Flack, L.K., 2006. Population ecology of hybrid mesquite (Prosopis species) in Western Australia: how does it differ from native range invasions and what are the implications for impacts and management. Biological Invasions 8, 727–741.

Van Wilgen, B.W., Richardson, D.M., 2014. Challenges and trade-offs in the management of invasive alien trees. Biological Invasions 16, 721–734.

Van Wilgen, B.W, Forsyth, G.G., Le Maitre, D.C., Wannenburgh, A., Kotzé, J.D.F., Van den Berg, E., Henderson, L., 2012. An assessment of the effectiveness of a large, national-scale invasive alien plant control strategy in South Africa. Biological Conservation 148, 28–38.

Versfeld, D.B., Le Maitre, D.C., Chapman, R.A., 1998. Alien invading plants and water resources in South Africa. Report no. TT 99/98. Water Research Commission, Pretoria pp. 276.

Voster, C.J., 2003. Simplified Geology, South Africa. Lesotho and Swaziland. Council for Geoscience, South Africa.

Walter, K.J., Armstrong, K.V., 2014. Benefits, threats and potential of *Prosopis* in South India. Forests, Trees and Livelihoods 23, 232–247.

Wise, R.M., Van Wilgen, B.W., Le Maitre, D.C., 2012. Costs, benefits and management options for an invasive alien tree species: the case of mesquite in the Northern Cape, South Africa. Journal of Arid Environments 84, 80–90.

Zachariades, C., Hoffmann, J.H., Roberts, A.P., 2011. Biological control of mesquite (*Prosopis* species) (*Fabaceae*) in South Africa. African Entomology 19, 402–415.

Zimmermann, H.G., 1991. Biological control of *Prosopis*, *Prosopis* spp. (*Fabaceae*), in South Africa. Agriculture, Ecosystems and Environment 37, 175–186.